

# Population Dynamics of *Aphis glycines* (Homoptera: Aphididae) and Impact of Natural Enemies in Northern China

JIN MIAO,<sup>1,2</sup> KONGMING WU,<sup>1</sup> KEITH R. HOPPER,<sup>3</sup> AND GUOXUN LI<sup>2</sup>

Environ. Entomol. 36(4): 840–848 (2007)

**ABSTRACT** Field surveys of soybean aphid, *Aphis glycines* Matsumura, and its natural enemies, as well as natural enemy enclosure experiments, were conducted during 2003 and 2004 in soybean fields near Langfang, China. In 2003, aphid density increased six-fold during 12 d in July from  $66 \pm 12$  per 10 plants to a seasonal peak of  $401 \pm 79$  per 10 plants. Aphid density remained high for another 10 d and declined during late July and early August. In 2004, aphid density increased 29-fold during 13 d in July from  $14 \pm 2$  per 10 plants to a seasonal peak of  $375 \pm 30$  per 10 plants. Unlike 2003, aphid density remained relatively high during late July and August, peaking again at  $296 \pm 31$  per 10 plants on 24 August. In both years, aphid density remained below economic injury level and seemed to be limited by natural enemies. Enclosure of natural enemies led to increases in *A. glycines* density in 2003 and 2004. In 2003, peak aphid densities in large- and medium-mesh cages were three- and seven-fold higher, respectively, than densities on uncaged plants. In 2004, peak aphid densities in large- and medium-mesh cages were 2-fold and 30-fold higher, respectively, than densities on uncaged plants in one experiment. In another experiment, peak aphid densities in large-, medium-, and small-mesh cages were 8-fold, 28-fold, and 68-fold higher, respectively, than densities on uncaged plants. Both predators and parasitoids were important in limiting aphid density. We compare our results with those from North America and discuss implications for biological control.

**KEY WORDS** *Aphis glycines*, natural enemies, biological control, enclosure experiment

Soybean, *Glycine max* L. Merrill, is among the most important domesticated plants. It has been cultivated for 4,500 yr in China, and its cultivation has been extended to many countries because it is easy to grow, has wide geographical adaptability, and has a broad spectrum of uses as human and animal food and in industrial and medical applications (Hymowitz 1970).

The soybean aphid, *Aphis glycines* Matsumura (Homoptera: Aphididae), sometimes causes significant yield losses on soybean in China (Wang et al. 1962, Yue et al. 1989, Wu et al. 1999, Sun et al. 2000). Besides direct feeding, *A. glycines* can vector viruses (Guo and Zhang 1989, Li and Pu 1991, Luo et al. 1991). The soybean aphid occurs in China, Japan, Philippines, South Korea, Indonesia, Malaysia, Thailand, Vietnam, and Russia (APPPC 1987). The soybean aphid has recently invaded Australia, the United States, and Canada (Venette and Ragsdale 2004).

A project to find, evaluate, and introduce Asian natural enemies of *A. glycines* into North America was initiated in 2001 (Heimpel et al. 2004). Although the

soybean aphid has many natural enemies in China, few experiments have been published quantifying the role of natural enemies in population regulation of this aphid in China (for review, see Wu et al. 2004). However, experiments on natural enemy impact in the region of origin should form an integral part of biological introduction projects (Hopper 1996, Hoelmer and Kirk 2005). Liu et al. (2004) reported a field survey and enclosure experiment addressing natural enemy impact on *A. glycines* near Langfang, China, in soybean in 2002. Here, we present an extension of this work during 2003 and 2004. The research included (1) measurement of the population dynamics of the aphid and its natural enemies on soybean and (2) field enclosure experiments to measure the impact of natural enemies on *A. glycines* population growth.

## Materials and Methods

**Location.** Experiments were conducted during the summers of 2003 and 2004 at Langfang Experimental Station, Chinese Academy of Agricultural Sciences, Hebei Province, China (116.4° E; 39.3° N).

**Field Survey.** The survey was carried out in a 0.20-ha soybean field (adjacent to cotton) planted after wheat harvest with cultivar “Zhonghuang-4” on 20 June 2003 and 2 July 2004. Sampling started in early July when alate aphids migrated into the field; at this time, the soybean seedlings were in the two-leaf

<sup>1</sup> State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing 100094, China.

<sup>2</sup> College of Plant Protection, Agricultural University of Hebei, Baoding 071001, China.

<sup>3</sup> Corresponding author: USDA-ARS, Beneficial Insect Introductions, Research Unit, 501 South Chapel St., Newark, DE 19713 (e-mail: Keith.Hopper@ars.usda.gov).

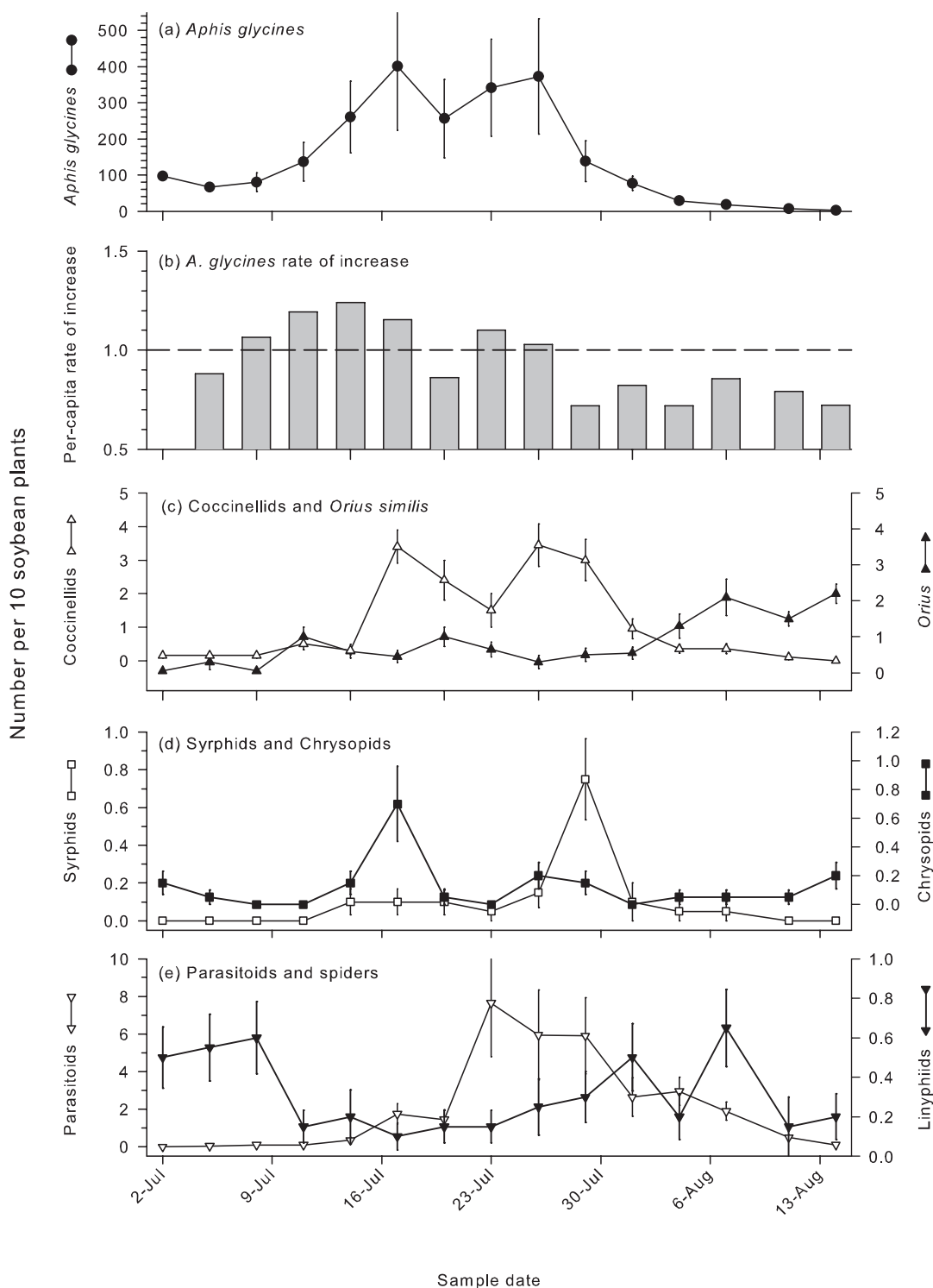


Fig. 1. Population dynamics of *A. glycines* and its natural enemies in Langfang in 2003.

stage. Twenty locations were selected as fixed sampling sites. Each one consisted of 10 plants, with at least one site being colonized by aphids. Samples

were collected every 2 d from July to September. Each plant was visually examined, and all insects were counted. Mummified aphids were collected,

and the numbers of each parasitoid species that emerged were recorded.

**Enclosure Experiment.** These experiments were done in a 0.53-ha soybean field planted with variety Zhonghuang-4. Soybean was planted on 7 July 2003 and on 27 June and 12 August 2004. The caged treatments were covered immediately after seedlings emerged to control infestation by aphids and natural enemies. No differences in plant growth were observed between caged and uncaged plants. When seedlings appeared, 30 plants were selected and tagged in each experimental unit (1 by 2-m area of soybean plants). These plants were infested artificially with a total of 60 aphids (alates and fourth instars; 2 aphids per plant). To infest plants, we collected the aphids from soybean fields and transferred the aphids to the experimental plants using a small brush.

In 2003, three levels of natural enemies enclosure were used, each sampled on 14 sample dates with four replicates per enclosure level per date: medium-mesh (1 by 1-mm holes) cages, large-mesh (2 by 2-mm holes) cages, and plants with no cages. In 2004, one experiment was done with the same three levels during 7 July to 2 August with 10 sample dates and four replicates per enclosure level per date and a second experiment that included a fourth level (small-mesh; 0.5 by 0.5-mm holes) was conducted from 23 August to 22 September with 10 sample dates and four replicates per enclosure level per date. Natural enemies had free access to aphids on uncaged plants but limited access to aphids on caged plants. The small mesh blocked emigration/immigration of aphids and natural enemies. The medium mesh allowed some emigration/immigration of aphids and parasitoids. The large mesh allowed emigration/immigration of aphids, parasitoids, and some predators.

Cages were polyester sacks 1 m wide, 2 m long, and 1.2 m high, supported on bamboo poles at each corner, with the bottom edge of the sacks buried in the soil. Insect numbers were sampled every 3 d until late September. Replicates were sampled destructively by cutting the plants, placing them in bags, and taking them to the laboratory for counting. All 30 plants were thoroughly examined, and all insects were counted. To ease comparison with numbers in the field survey, we report the numbers per 10 plants. Mummified aphids were collected, and the numbers and species of parasitoids that emerged were recorded. Vouchers of all species are kept at the Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing, China.

**Data Analysis.** Aphid population densities were non-normally distributed and therefore were log-transformed for analyses. For the field survey, we tested the effect of sample date on aphid density with a repeated-measures mixed-model analysis of variance (ANOVA), with date repeated within location, which was considered a random effect. We tested the relationship between the finite rate of increase of aphid populations and total densities of predators and of parasitoids using Kendall's correlation coefficient (Kendall 1938). For field measurements, the finite rate

of increase was calculated as  $\lambda = (N_{t+\Delta t}/N_t)^{1/\Delta t}$  where  $N_t$  is the density of aphids at time  $t$ , and  $\Delta t$  is the time between samples (Lotka 1925). This was compared with the maximum finite rate of increase from life table data measured in the laboratory at a range of temperatures (unpublished data). For the laboratory data, the finite rate of increase was calculated as  $\lambda = \sum l_x m_x / T$ , where  $l_x$  and  $m_x$  are the age-specific survivorship and birth rate, and  $T$  is the generation time (Lotka 1925). For the enclosure experiments, we tested the effects of enclosure level, date, and their interaction on aphid density and parasitoid density with ANOVA. For all analyses, we used SAS/STAT version 9.1 (SAS Institute, Cary, NC).

## Results

**Aphis glycines Population Dynamics.** In 2003, the population density of soybean aphid varied with sampling date (Fig. 1a;  $F = 34.3$ ;  $df = 14,266$ ;  $P < 0.0001$ ). Aphid density increased six-fold during 12 d in July from a low of  $66 \pm 12$  per 10 plants on 5 July to a seasonal peak of  $401 \pm 79$  per 10 plants on 17 July. Aphid density remained high for another 10 d and declined in late July and early August. The maximum finite rate of increase was 1.24 per day (Fig. 1b), which is 87% of the maximum expected from laboratory studies on soybean aphid from Langfang (unpublished data).

In 2004, the population density of soybean aphid again varied with sampling date (Fig. 2a;  $F = 31.4$ ;  $df = 18,342$ ;  $P < 0.0001$ ). Aphid density increased 29-fold during 13 d from a low of  $14 \pm 2$  per 10 plants on 15 July to a seasonal peak of  $375 \pm 30$  per 10 plants on 28 July. Unlike 2003, aphid density remained relatively high during late July and August, peaking again at  $296 \pm 31$  per 10 plants on 24 August. Aphid density declined after this second peak. The maximum rate of increase was 1.73 per day (Fig. 2b), which is 121% of the maximum expected from laboratory studies on soybean aphid from Langfang (unpublished data).

**Abundances and Dynamics of *A. glycines* Natural Enemies.** Sixteen species of aphid natural enemies, including 3 parasitoids and 13 predators, were found in field surveys in 2003 and 2004 (Table 1). The parasitoids were *Lysiphlebus* sp., *Binodoxys communis* (Gahan) and *Aphelinus* sp. and were reared from *A. glycines*. The hyperparasitoid, *Syrphophagus aphidivorus* (Mayr) (Hymenoptera: Encyrtidae), was found parasitizing these primary parasitoids. The main aphid predators were *Propylaea japonica* (Thunberg), *Orius similis* Zheng, *Chrysopa septempunctata* Wesm., *Chrysopa sinica* Tjeder, *Metasyrphus corollae* (F.), *Epistrophe balteata* de Geer, and *Hylyphantus graminicola* (Sundevall). All these predators attack aphids, and most have been reported to prey on soybean aphid (for review, see Wu et al. 2004).

In 2003, coccinellids, chiefly *P. japonica*, were the most abundant predators, followed by *O. similis*, linyphiid spiders, chrysopids, and syrphids (Fig. 1c-e; Table 1). Parasitized aphids were more common than

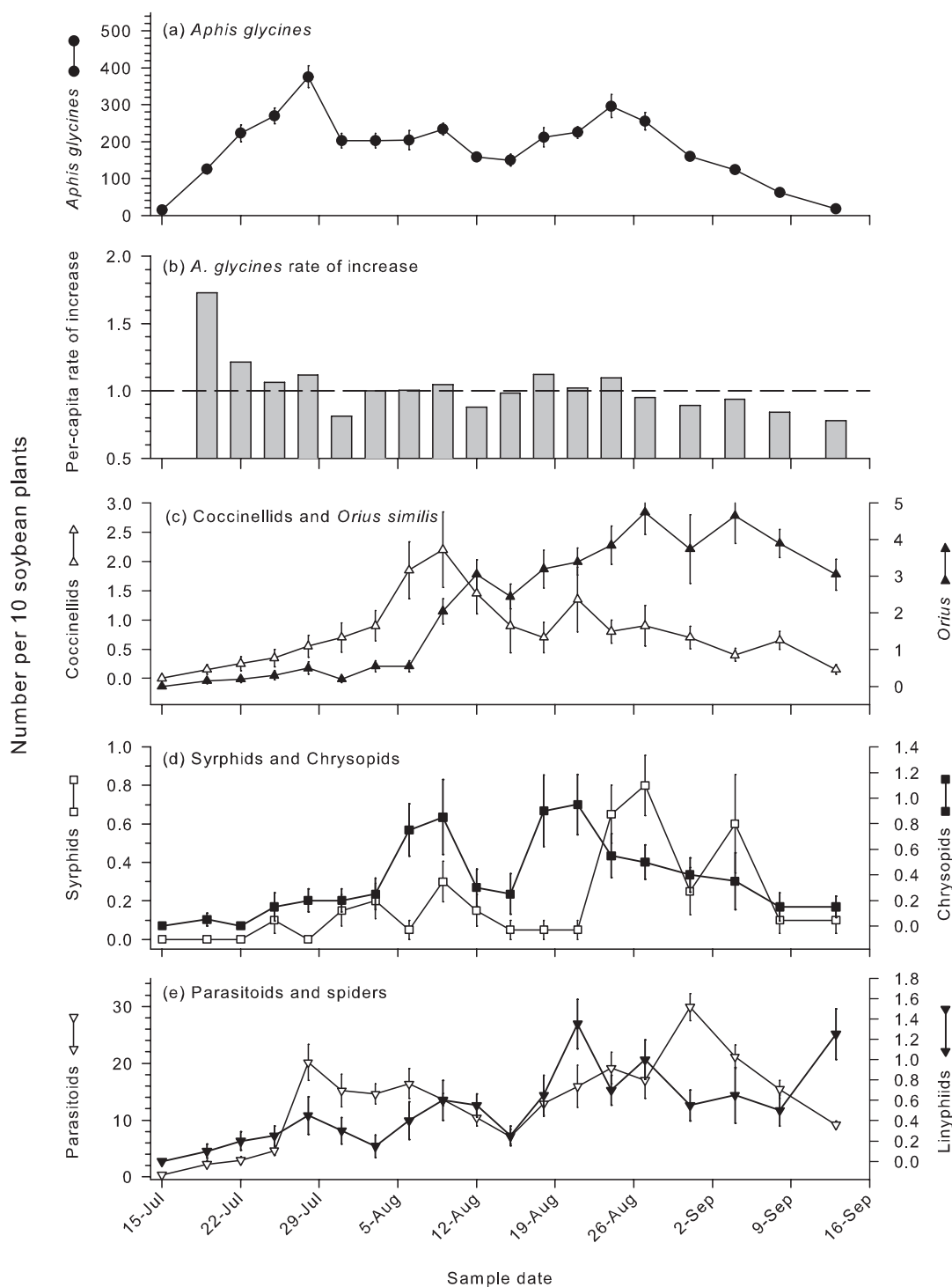


Fig. 2. Population dynamics of *A. glycines* and its natural enemies in Langfang in 2004.

predators. Maximum parasitism was  $14 \pm 6\%$  and occurred on 11 August; parasitism was  $<10\%$  throughout July. The rate of increase of *A. glycines* did not correlate with the total density of predators (Kendall's

$\tau = -0.32$ ,  $n = 14$ ,  $P = 0.11$ ) but correlated negatively with the total density of parasitized aphids (estimated from number mummified; Kendall's  $\tau = -0.42$ ,  $n = 14$ ,  $P = 0.04$ ; Fig. 3a).

Table 1. Natural enemies of *A. glycines* in field surveys at Langfang Experimental Station in 2003 and 2004

Category	Order	Family	Species	Seasonal mean (per 10 plants)		Seasonal max (per 10 plants)	
				2003	2004	2003	2004
Parasitoids	Hymenoptera	Aphelinidae	<i>Aphelinus</i> sp.	2.1	13.1	7.7	29.9
		Braconidae	<i>Lysiphlebus</i> sp.				
Predators	Araneae	Linyphiidae	<i>Binodoxys communis</i> (Gahan)	0.3	0.5	0.7	1.4
			<i>Hylyphantes graminicola</i> (Sundevall)				
	Coleoptera	Coccinellidae	<i>Propylaea japonica</i> (Thunberg)	1.1	0.8	3.5	2.2
			<i>Scymnus hoffmanni</i> Weise				
			<i>Epistrophe balteata</i> de Geer	0.1	0.2	0.8	0.7
	Diptera	Syrphidae	<i>Paragus quadrfasciatus</i> Meigen				
			<i>Paragus tibialis</i> (Fallén)				
			<i>Sphaerophoria</i> sp.				
	Hemiptera	Anthocoridae	<i>Orius similis</i> Zheng	0.8	2.1	2.2	4.8
		Nabidae	<i>Nabis sinoferus</i> Hsiao	—	—	—	—
Neuroptera	Chrysopidae		<i>Chrysopa shansiensis</i> Kawa	0.1	0.4	0.2	1.0
			<i>Chrysopa septempunctata</i> Pleshanov				
			<i>Chrysopa sinica</i> Tjeder				
			<i>Chrysopa formosa</i> Brauer				

Numbers on 10 whole plants were sampled at 20 locations at 3-d intervals from 2 July to 14 Aug. 2003 and 15 July to 13 Sept. 2004. Values for parasitoids are no. of parasitized (mummified) aphids.

In 2004, *O. similis* was the most abundant predator, followed by coccinellids, linyphiid spiders, chrysopids, and syrphids (Fig. 2c–e; Table 1). Densities of predators and parasitized aphids were higher in 2004 than in 2003 (Table 1). Parasitized aphids were more common than predators. Maximum parasitism was  $48 \pm 4\%$  and occurred at the end of the season (13 September); parasitism was  $<10\%$  until 31 August. The rate of increase of *A. glycines* correlated negatively with total

density of predators (Kendall's  $\tau = -0.42$ ,  $n = 18$ ,  $P = 0.02$ ) and total density of parasitoids (Kendall's  $\tau = -0.56$ ,  $P = 0.001$ ; Fig. 3b).

**Impact of *A. glycines* Natural Enemies in Enclosure Experiment.** Enclosure of natural enemies led to increases in *A. glycines* density in both 2003 and 2004 (Fig. 4; Table 2).

In 2003, peak aphid densities in large- and medium-mesh cages were three- and seven-fold higher, respectively, than densities on uncaged plants (Fig. 4a). Aphid density differed among enclosure levels by 20 August, and densities continued to diverge until mid-September when numbers on caged plants began to decline. The maximum rates of increase in large-mesh and medium-mesh cages were 1.53 and 1.72 per day, respectively, which are 107 and 121% of the maximum expected from laboratory studies on soybean aphid from Langfang. The peak aphid density on uncaged plants,  $237 \pm 28$  per 10 plants, was  $\approx 60\%$  of the peak observed in the field survey ( $401 \pm 79$  per 10 plants) and occurred later in the season, 8 September versus 17 July. The maximum rate of increase on uncaged plants was 1.47, which is 103% of the maximum expected from laboratory studies. However, the growth rate on uncaged plants became low or negative within 10 d of the beginning of the experiment, whereas the growth rate on caged plants continued positive until mid-September.

In 2004 in experiment 1, peak aphid densities in large- and medium-mesh cages were 2- and 30-fold higher, respectively, than densities on uncaged plants (Fig. 4b). Aphid density differed among enclosure levels by the first sample date on 7 July, and densities continued to diverge until the end of experiment 1 at the beginning of August. The maximum rates of increase in large and medium-mesh cages were 1.29 and 1.67 per day, which are 91 and 117% of the maximum expected from laboratory studies. In 2004 in experiment 2, peak aphid densities in large-, medium-, and small-mesh cages were 8-, 28-, and 68-fold higher,

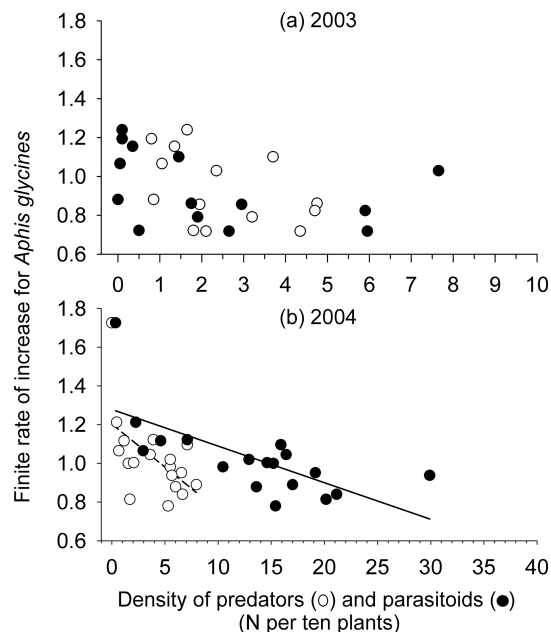


Fig. 3. Finite rate of increase for *A. glycines* versus densities of predators (○) and parasitized (mummified) aphids (●) in Langfang in 2003 and 2004. Lines for 2004 are linear regressions for predators (dashed;  $F = 7.0$ ;  $df = 1,16$ ;  $P = 0.02$ ;  $R^2 = 0.30$ ) and parasitoids (solid;  $F = 14.1$ ;  $df = 1,16$ ;  $P = 0.002$ ;  $R^2 = 0.47$ ) analyzed separately.

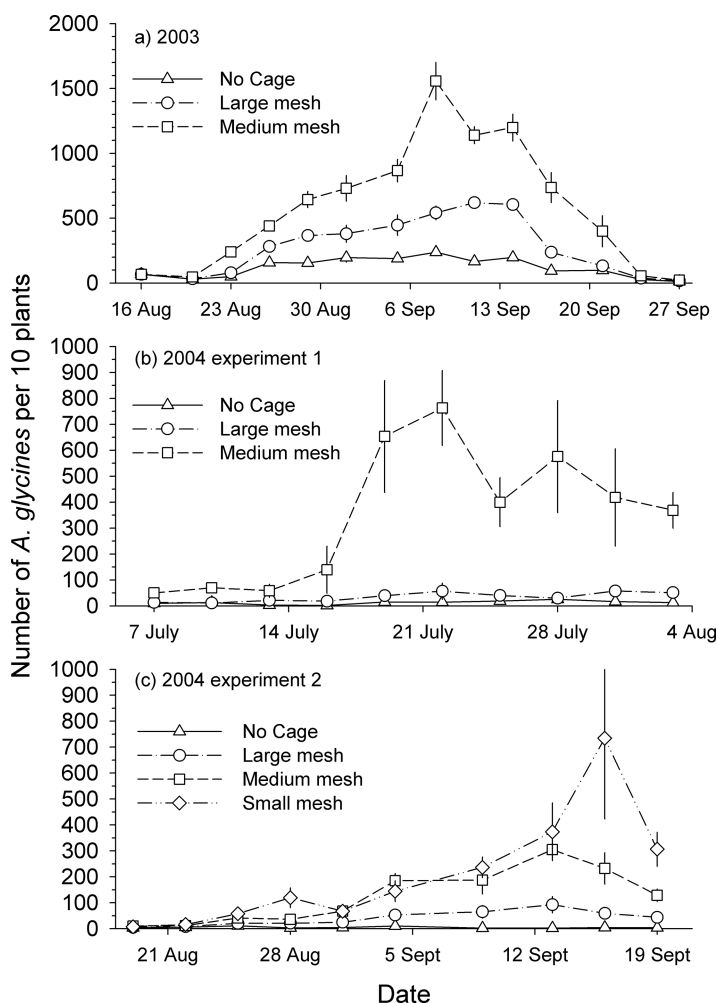


Fig. 4. Effect of natural enemy exclusion on density and rate of increase of *A. glycines* in Langfang in 2003 and 2004.

respectively, than densities on uncaged plants (Fig. 4c). Aphid density differed among exclusion levels by the second sample date on 26 August, and densities continued to diverge until mid-September when numbers on caged plants began to decline. The maximum rates of increase in large-mesh, medium-mesh, and small-mesh cages were 1.38, 1.52, and 1.53 per day, respectively, which are 96, 106, and 107% of the maximum expected from laboratory studies. The peak aphid density on uncaged plants,  $25 \pm 6$  per 10 plants, was  $\approx 15$ -fold lower than the peak observed in the field survey ( $375 \pm 30$  per 10 plants). The maximum rate of increase on uncaged plants was 1.27, which is 89% of the maximum expected from laboratory studies. The growth rate on uncaged plants became low or negative early in both experiments, whereas the growth rate in all caged treatments continued positive much longer in each experiment (Fig. 4b and c).

**Natural Enemies of *A. glycines* in Field Exclusion Experiments.** We found three species of parasitoids, *Aphelinus* sp., *B. communis*, and *Lysiphlebus* sp., in the medium-mesh cages, and these species plus the pred-

ator, *O. similis*, in the large-mesh cages, but we found no natural enemies in small-mesh cages. The exclusion level affected parasitoid density (Table 2).

We found 19 species of predators and parasitoids on uncaged plants, which included the species found in the field survey (Table 1), and in addition, *Syrphus corollae* F. (Diptera: Syrphidae), an *Aphidoletes* species (Diptera: Cecidomyiidae), *Geocoris pallidipennis* (Costa) (Hemiptera: Geocoridae), and *Deraeocoris punctulatus* (Fallén) (Hemiptera: Miridae).

## Discussion

The negative correlations between the population growth of *A. glycines* on one hand and the densities of predators and parasitoids on the other suggest that natural enemies limited population growth of *A. glycines* at the Langfang Experimental Station in 2003 and 2004. The effect of natural enemy exclusion confirms this suggestion. Furthermore, the differences in aphid density and rate of increase among the different mesh cages provide some detail about the roles of different



Table 2. ANOVA for effects of natural enemy exclusion level and sample date on abundances of *A. glycines* and its parasitoids

Year	Dependent variable	Factor	df	F	P
2003	Aphid density	Exclusion level	2	405.9	<0.0001
		Date	13	297.0	<0.0001
		Exclusion $\times$ date	26	8.0	<0.0001
		Error	126	—	—
2004 (experiment 1)	Aphid density	Exclusion level	2	165.2	<0.0001
		Date	9	10.3	<0.0001
		Exclusion $\times$ date	18	2.2	0.009
		Error	90	—	—
2004 (experiment 2)	Aphid density	Exclusion level	3	186.0	<0.0001
		Date	9	29.5	<0.0001
		Exclusion $\times$ date	27	4.7	<0.0001
		Error	120	—	—
2003	Parasitoid density	Exclusion level	2	43.7	<0.0001
		Date	13	180.2	<0.0001
		Exclusion $\times$ date	26	2.0	0.005
		Error	126	—	—
2004 (experiment 1)	Parasitoid density	Exclusion level	2	62.2	<0.0001
		Date	9	1.8	0.08
		Exclusion $\times$ date	18	1.4	0.14
		Error	90	—	—
2004 (experiment 2)	Parasitoid density	Exclusion level	3	40.3	<0.0001
		Date	9	27.7	<0.0001
		Exclusion $\times$ date	27	4.6	<0.0001
		Error	120	—	—

groups of natural enemies. Medium-mesh cages, in which parasitoids but not predators were found in all experiments, had higher aphid densities than large-mesh cages and lower aphid densities than small-mesh cages, indicating that parasitoids alone had a significant effect on aphid density (Fig. 3). In 2003, large-mesh cages, in which the predator, *O. similis*, and parasitoids were found had lower aphid densities than uncaged plants, indicating that this predator also significantly affected aphid density. In experiment 1 in 2004, the greatest difference was between medium-mesh cages on one hand and large-mesh cages and uncaged plants on the other, which suggests that exclusion of predators was most important. However, in experiment 2, medium-mesh cages (with parasitoids) only differed from small-mesh cages at the end of the season, when parasitism levels were high.

Three hypotheses could explain the greater growth rate of *A. glycines* populations in cages: (1) microclimate may have differed among treatments, and the differences could have affected plant growth and aphid reproduction or survival; (2) cages may have reduced aphid emigration, causing aphid density to build up; and (3) cages may have reduced aphid mortality by excluding natural enemies. Although experiments on *Diuraphis noxia* (Mordvilko) (Hemiptera: Aphididae) with similar cages eliminated hypotheses 1 and 2 (Hopper et al. 1994, 1995, Basky and Hopper 2000), these explanations might still apply in this experiment. However, blocked emigration cannot explain the build up of soybean aphids in large- and medium-mesh cages because aphid density was higher than on plants without cages, yet aphids could disperse from these cages. Several natural enemies were found in large and medium-mesh cages, but no natural enemies were found in the small-mesh cages. Thus, these natural enemies were evidently able to enter and leave

large- and medium-mesh cages, and the aphid density was lower in these cages than in the small-mesh cages. Plant growth was not obviously affected by the cages, but effects of microclimate cannot be eliminated. However, the differences between the aphid population growth rate among several mesh sizes suggests that natural enemy exclusion is a more likely hypothesis.

More and different species of natural enemies were found in this research than in the previous study at Langfang (Liu et al. 2004), suggesting that the suite of natural enemies changes between years. The abundance of each species and each group of natural enemies varied during the season in the results reported here (Figs. 1 and 2), and no individual species of natural enemy showed a significant negative correlation with aphid rate of increase. However, the overall abundance of natural enemies was more constant and showed a negative correlation with aphid rate of increase, suggesting that the combined effect of all the *A. glycines* natural enemies was important in limiting its rate of increase and abundance.

The same families, and often the same genera, of predators attack *A. glycines* in North America, although the species differ (Fox et al. 2004, 2005, Rutledge et al. 2004, Costamagna and Landis 2006, Desneux et al. 2006, Mignault et al. 2006). Interestingly, *Orius insidiosus* (Say) (Hemiptera: Anthocoridae), a congener of *O. similis* found in our research, was the most abundant predator in one North American field study (Desneux et al. 2006), and laboratory experiments suggested that it could suppress *A. glycines* population growth (Rutledge and O'Neil 2005). However, *O. insidiosus* often died or ceased attack when exposed to cornicular exudates from *A. glycines*, suggesting that soybean aphid may be able to defend itself from attack by this species (Butler and O'Neil 2006).

Nonetheless, generalist predators have been shown to suppress *A. glycines* population growth in North America (Fox et al. 2005, Rutledge and O'Neil 2005, Costamagna and Landis 2006, Desneux et al. 2006). Furthermore, entomopathogenic fungi can also be important causes of mortality (Nielsen and Hajek 2005). However, the impact of generalist predators and pathogens has been variable (Fox et al. 2005) (Nielsen and Hajek 2005). These results suggest that conservation and augmentation of predators and pathogens native to North America should be pursued for management of *A. glycines*. However, parasitoids have been rare in studies of *A. glycines* in North America, although they seem to be important in Asia. The lack of parasitoid impact in North America, together with the potential host specificity of parasitoids, suggest that we should concentrate on parasitoids as candidates for introduction.

### Acknowledgments

K.-J. Lin provided insightful suggestions and help during the study. We thank X.-X. Chen, Zhejiang University, and J. Liu, Northeast Agricultural University, for identifying parasitoids and predators and G. Z. Khan, Nuclear Institute of Agriculture, Tandojam, Pakistan, J. Ruberson, University of Georgia, and an anonymous reviewer for comments on this manuscript.

### References Cited

- Asian and Pacific Plant Protection Commission (FAO). 1987. Insect pests of economic significance affecting major crops of the countries in Asia and the Pacific region. Regional FAO Office for Asia and the Pacific (RAPA), Bangkok, Thailand.
- Basky, Z., and K. R. Hopper. 2000. Impact of plant density and natural enemy exclusion on abundance of *Diuraphis noxia* (Kurdjumov) and *Rhopalosiphum padi* (L.) (Hom., Aphididae) in Hungary. *J. Appl. Entomol.* 124: 99–103.
- Butler, C. D., and R. J. O'Neil. 2006. Defensive response of soybean aphid (Hemiptera: Aphididae) to predation by insidious flower bug (Hemiptera: Anthoridae). *Ann. Entomol. Soc. Am.* 99: 317–320.
- Costamagna, A. C., and D. A. Landis. 2006. Predators exert top-down control of soybean aphid across a gradient of agricultural management systems. *Ecol. Appl.* 16: 1619–1628.
- Desneux, N., R. J. O'Neil, and H. J. S. Yoo. 2006. Suppression of population growth of the soybean aphid, *Aphis glycines* Matsumura, by predators: the identification of a key predator and the effects of prey dispersion, predator abundance, and temperature. *Environ. Entomol.* 35: 1342–1349.
- Fox, T. B., D. A. Landis, F. F. Cardoso, and C. D. Difonzo. 2004. Predators suppress *Aphis glycines* Matsumura population growth in soybean. *Environ. Entomol.* 33: 608–618.
- Fox, T. B., D. A. Landis, F. F. Cardoso, and C. D. Difonzo. 2005. Impact of predation on establishment of the soybean aphid, *Aphis glycines*, in soybean, *Glycine max.* *Biocontrol* 50: 545–563.
- Guo, J. Q., and M. H. Zhang. 1989. Study on the important vectors of soybean mosaic virus and their transmission efficiency. *Soybean Sci.* 8: 55–63.
- Heimpel, G. E., D. W. Ragsdale, R. Venette, K. R. Hopper, R. J. O'Neil, C. E. Rutledge, and Z. S. Wu. 2004. Prospects for importation biological control of the soybean aphid: anticipating potential costs and benefits. *Ann. Entomol. Soc. Am.* 97: 249–258.
- Hoelmer, K. A., and A. A. Kirk. 2005. Selecting arthropod biological control agents against arthropod pests: can the science be improved to decrease the risk of releasing ineffective agents? *Biol. Control* 34: 255–264.
- Hopper, K. R. 1996. Making biological control introductions more effective, pp. 61–76. In J. K. Waage (ed.), *Biological control introductions: opportunities for improved crop production*. British Crop Protection Council Symposium Proceedings No. 67. British Crop Protection Council, Brighton, UK.
- Hopper, K. R., T. Randolph, J. Boylan, A. Cepaitis, X. Fauvergue, J. Gould, and D. Prokrym. 1994. Natural enemy impact on *Diuraphis noxia* (Mordvilko) (Homoptera: Aphididae) in northeastern Colorado compared to southern France. Proceedings 6th Russian Wheat Aphid Workshop, 23–25 January 1994, Fort Collins, CO.
- Hopper, K. R., S. Aidara, S. Agret, J. Cabal, D. Coutinot, R. Dabire, C. Lesieux, G. Kirk, S. Reichert, and F. Tronchetti. 1995. Natural enemy impact on the abundance of *Diuraphis noxia* (Homoptera: Aphididae) in wheat in southern France. *Environ. Entomol.* 24: 402–408.
- Hymowitz, T. 1970. On the domestication of the soybean. *Econ. Botany*. 24: 408–421.
- Kendall, M. G. 1938. A new measure of rank correlation. *Biometrika* 30: 81–93.
- Li, W. M., and Z. Q. Pu. 1991. Population dynamics of aphids and epidemics of soybean mosaic virus in summer sown soybean fields. *Act. Phytophyl. Sin.* 18: 123–126.
- Liu, J., K. Wu, K. R. Hopper, and K. Zhao. 2004. Population dynamics of *Aphis glycines* (Homoptera: Aphididae) and its natural enemies in soybean in Northern China. *Ann. Entomol. Soc. Am.* 97: 235–239.
- Lotka, A. J. 1925. *Elements of physical biology*. Williams and Wilkins, Baltimore, MD.
- Luo, R. W., Y. F. Shang, C. L. Yang, J. H. Zhao, and C. S. Li. 1991. Study on the epidemiology and prediction of soybean mosaic virus. *Act. Phytophyl. Sin.* 18: 267–271.
- Mignault, M. P., M. Roy, and J. Brodeur. 2006. Soybean aphid predators in Quebec and the suitability of *Aphis glycines* as prey for three Coccinellidae. *Biocontrol* 51: 89–106.
- Nielsen, C., and A. E. Hajek. 2005. Control of invasive soybean aphid, *Aphis glycines* (Hemiptera: Aphididae), populations by existing natural enemies in New York State, with emphasis on entomopathogenic fungi. *Environ. Entomol.* 34: 1036–1047.
- Rutledge, C. E., and R. J. O'Neil. 2005. *Orius insidiosus* (Say) as a predator of the soybean aphid, *Aphis glycines* Matsumura. *Biol. Control* 33: 56–64.
- Rutledge, C. E., R. J. O'Neil, T. B. Fox, and D. A. Landis. 2004. Soybean aphid predators and their use in integrated pest management. *Ann. Entomol. Soc. Am.* 97: 240–248.
- Sun, B., S. B. Liang, and W. X. Zhao. 2000. Outbreak of the soybean aphid in Suihua prefecture in 1998 and its control methods. *Soybean Bull.* 1: 5.
- Venette, R. C., and D. W. Ragsdale. 2004. Assessing the invasion by soybean aphid (Homoptera: Aphididae): where will it end? *Ann. Entomol. Soc. Am.* 97: 219–226.
- Wang, C. L., N. I. Siang, G. S. Chang, and H. F. Chu. 1962. Studies on the soybean aphid, *Aphis glycines* Matsumura. *Act. Entomol. Sin.* 11: 31–44.



- Wu, X. B., W. J. Ni, and P. J. Liu. 1999. Occurrence and control of the soybean aphid, *Aphis glycines* Matsumura. Chin. J. Biol. Control 6: 20.
- Wu, Z. S., D. Schenk-Hamlin, W. Y. Zhan, D. W. Ragsdale, and G. E. Heimpel. 2004. The soybean aphid in China: a historical review. Ann. Entomol. Soc. Am. 97: 209–218.
- Yue, D. R., S. G. Guo, and Y. L. Shan. 1989. Resistance of wild soybean *Glycine soja* to *Aphis glycines*. I. Screening for resistant varieties. Jilin Agric. Sci. 3: 15–19.

*Received for publication 21 June 2006; accepted 19 April 2007.*

---